

COMPARATIVE MORPHOLOGY OF THE BUTTERFLY FORELEG COXA AND TROCHANTER (LEPIDOPTERA) AND ITS SYSTEMATIC IMPLICATIONS

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Abstract.—I describe and illustrate five qualitatively distinct forms of butterfly foreleg coxa, trochanter, and basal femur, and give the distribution of each type by sex for the butterfly families. I code this variation in a character matrix of four characters with 9 character states, from which I derive a most parsimonious cladogram with four monophyletic groups: (1) Styginae (Riodinidae), (2) Hamearinae (in part) + Styginae + Riodininae + Euselasiinae (Riodinidae), (3) Lipteninae + Poritinae + Liphyrinae + Miletinae + Curetinae (Lycaenidae), and (4) Riodinidae + Libytheidae + Nymphalidae. The second and third groups have not been recognized previously as monophyletic. The fourth supports previous results based on other leg characters, but is inconsistent with most published phylogenies to the butterfly families. Contrary to previous reports, the forecoxa of male *Styx infernalis* (Riodinidae: Styginae) extends beyond the trochanter, but this extension is smaller than in most other riodinids. I also show that the male forelegs of *Curetis* (Lycaenidae: Curetinae) and Riodinidae are qualitatively different, a result that does not support the hypothesis that these two taxa are sister groups.

Key Words: leg characters, butterfly, cladogram

For more than 125 years, classification of the butterfly families has relied heavily on foreleg characters, particularly those of the tarsus (Bates 1861, Ford 1945), but morphology of the male foreleg coxa and trochanter has also been used in butterfly higher classification (cf. Borror et al. 1981 for an introduction to insect leg morphology). Godman and Salvin (1879-1901) discovered that the male forecoxa of riodinids extends beyond its articulation with the trochanter, and Stichel (1910-1911) and Ehrlich (1958b) characterized the Riodinidae (Ehrlich's Riodininae), in part, by this structure. Ehrlich also erected a new monobasic "subfamily"—of rank equal to the Lycaenidae (his Lycaeninae) and Riodinidae—for *Styx infernalis* Staudinger because its

male forecoxa does not extend spinelike beyond the trochanter and because it differs from riodinids in a few other structures. Scott (1985) proposed that *Curetis* (a genus that Ehrlich had considered to be a lycaenid) and Riodinidae (his Riodininae without *Styx*) are sister groups because both have the male foreleg coxa extending beyond the trochanter.

The few published figures of foreleg coxae and trochanters lack detail (e.g. Ehrlich 1958a, b, Scott 1986), and I propose to solve this problem with the use of a scanning electron microscope (SEM). It is clearly important that the morphology of these structures be well documented if they are to be used in constructing familial classifications of the butterflies. The first purpose of this paper

is to describe and illustrate the foreleg coxa, trochanter, and basal femur of males and females from the different butterfly families.

The second purpose of this paper is to assess the morphologic and phylogenetic hypotheses of Ehrlich (1958b) and Scott (1985). Specifically, I (1) check Ehrlich's statement that the male foreleg coxa of *Styx* does not extend beyond its articulation with the trochanter and (2) assess Scott's proposal that *Curetis* and the Riodinidae are sister groups, based in part on the observation that in both taxa the male forecoxa extends beyond the trochanter.

The third purpose of this paper is to use variation of the foreleg coxa and trochanter among higher taxa to further our understanding of butterfly phylogeny. I code this variation in a character matrix, derive a most parsimonious cladogram, determine whether it is consistent with published phylogenies (Ehrlich 1958b, Kristensen 1976, Scott 1985), and assess the monophyly of some higher taxa.

MATERIALS AND METHODS

Because foreleg coxae are difficult to remove from dried specimens without breakage, in most cases I wetted the whole body (after removing the wings) in 80% ethanol, soaked it in 10% potassium hydroxide at room temperature for 24–48 hours, and transferred it to 80% ethanol. I then removed both forelegs, and brushed and scraped off as many scales as possible with forceps and a brush with stout bristles. In some cases where scales were particularly hard to remove, I transferred the legs to acetone, which helped to loosen the scales. At this point I examined specimens with a binocular stereomicroscope, which is often times sufficient to determine structures.

For examination with an SEM, I soaked foreleg coxa, trochanter, and femur preparations in absolute ethanol for 5–10 minutes, and mounted them on stubs in various aspects. I mounted some laterally so that they presented either an outside or inside lateral aspect, others as an upright triangle,

which provided a posterior aspect in addition to both lateral aspects, and still others as parts of segments to show particular structures. I glued the specimens at the origin of the coxa and/or at the distal end of the femur, and the stubs were coated with carbon and gold.

RESULTS

There are five qualitatively distinct forms of foreleg coxa, trochanter, and femur; all five occur in males while two are found in females. The foreleg coxa, trochanter, and femur in butterflies have a complex three-dimensional morphology that is difficult to communicate on a two-dimensional printed page. I describe the first leg type in detail using pictures from inside lateral, posterior, outside lateral, and anterior aspects, and note some of the major morphological "landmarks" and shapes. I then describe the other leg types by focusing on how they differ from the first one. I illustrate specimens representing diverse taxonomic groups to show some of the quantitative variation within each foreleg type. Under this description, I list genera by family in which I found it. Because distribution of the different foreleg types differs in the sexes, I list distributions in males and females separately. If I examined more than one specimen of one sex in a genus, then I place an asterisk (*) after the generic name.

The familial classification follows Ehrlich (1958b) except for the Lycaenidae and Riodinidae, for which I follow Eliot (1973) and Harvey (1987), respectively. Harvey divided the Riodinidae into the subfamilies Styginae, Corrachiinae, Hamearinae, Euselasiinae, and Riodiniinae. The Corrachiinae contains a single rare species that I have not had an opportunity to examine.

TYPE I

Morphology.—*Foreleg coxa*: A tapering tubular structure that is shaped very differently than the midleg or hindleg coxa. Ehrlich (1958a) reported that the coxa is grooved

laterally in the monarch (*Danaus plexippus* Linnaeus), an observation that I believe to be incorrect. I list each morphological structure by letter, and use that letter to designate it in the figures.

The foreleg coxa has a pair of posterior pointing mid- to ventro-lateral processes that articulate with the trochanter. The hinge formed between these processes and the trochanter allows leg movement along the longitudinal plane. (A) One process is on the inner lateral side (Figs. 1–4) and (B) the other on the outer lateral side (Figs. 5–8).

(C) There are two rod-like “tendons” within the coxa that attach distally to the trochanter, one dorsally, the other ventrally (not illustrated). When the coxa and trochanter are separated, the tendons usually remain attached to the trochanter. They are best seen with transmitted light under a binocular stereomicroscope.

Foreleg trochanter: A complexly curved three-dimensional segment.

(D) There are a pair of prongs on the dorsal basal edge of the trochanter (Figs. 9–12). They attach to the dorsal “tendon” of the coxa. The prongs vary considerably in extent, and are reduced to two bumps in some Nymphalidae (Fig. 12).

(E) The outside surface of the trochanter is rounded in posterior aspect (Figs. 9–12), and is indented anteriorly in lateral aspect where the posterior coxa process articulates with it (Figs. 5–8).

(F) The inner surface of the trochanter is slightly concave in posterior aspect (Figs. 9–12), and is slightly indented ventrally where it articulates with the femur process (Figs. 1–4).

(G) There is a slit/groove that extends dorsally from the posterior edge of the indentation for the femur process and that forms the posterior edge of the concave area on the inner surface of the trochanter (Figs. 1–3, 9–10). I presume that this slit/groove allows the leg some lateral flexibility in movement.

There are three clusters of small trichoid sensilla (5 or more sensilla, less than 40 mi-

crotons in length except in some larger butterflies, such as Papilionidae) on the trochanter. (H) A cluster on the lateral indentation just anterior and ventral to the inside dorsal prong of the trochanter (Figs. 1–4, 9–12). (I) A cluster on the lateral indentation just anterior and ventral to the outside dorsal prong of the trochanter (Figs. 5–8, 9–12). (J) A third cluster just below the articulation of the coxa process on the anterior face of the trochanter. It can be seen from an inside lateral aspect (Figs. 1–4), but is best seen in anterior aspect (Figs. 13–14). I presume that these trichoid sensilla are mechanoreceptors, at least in part, because they occur where movements of the trochanter would cause them to come into contact with the coxa. There are also other trichoid sensilla scattered over the foreleg, but they occur singly or in a cluster of two, and are often longer than 40 microns in length.

Foreleg femur: A simple tubular structure at its basal end, where it connects to the trochanter.

(K) There is a basal process on the posterior inner face of the femur (Figs. 1–4, 9–11). This process may be rounded or somewhat tapered to a point.

Male distribution.—*Hesperiidae:* *Poanes* Scudder, *Megathymus* Scudder, *Autochton* Hübner, *Epargyreus* Hübner.

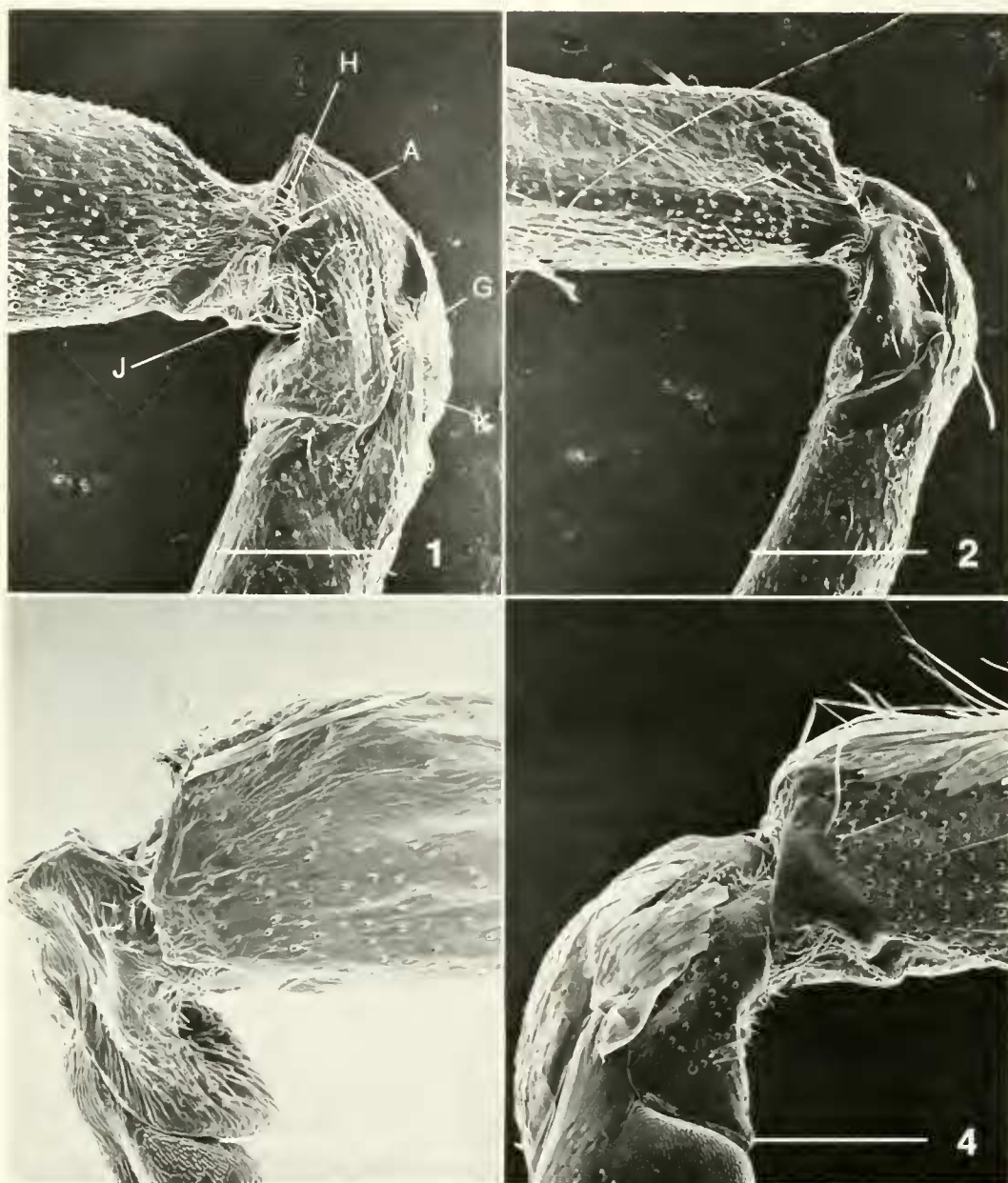
Papilionidae: *Papilio* Linnaeus, *Battus* Scopoli, *Eurytides* Hübner, *Parnassius* Latreille.

Pieridae: *Eurema** Hübner, *Phoebis* Hübner, *Colotis* Hübner, *Pieris** Schrank, *Euchloe* Hübner, *Dismorphia* Hübner.

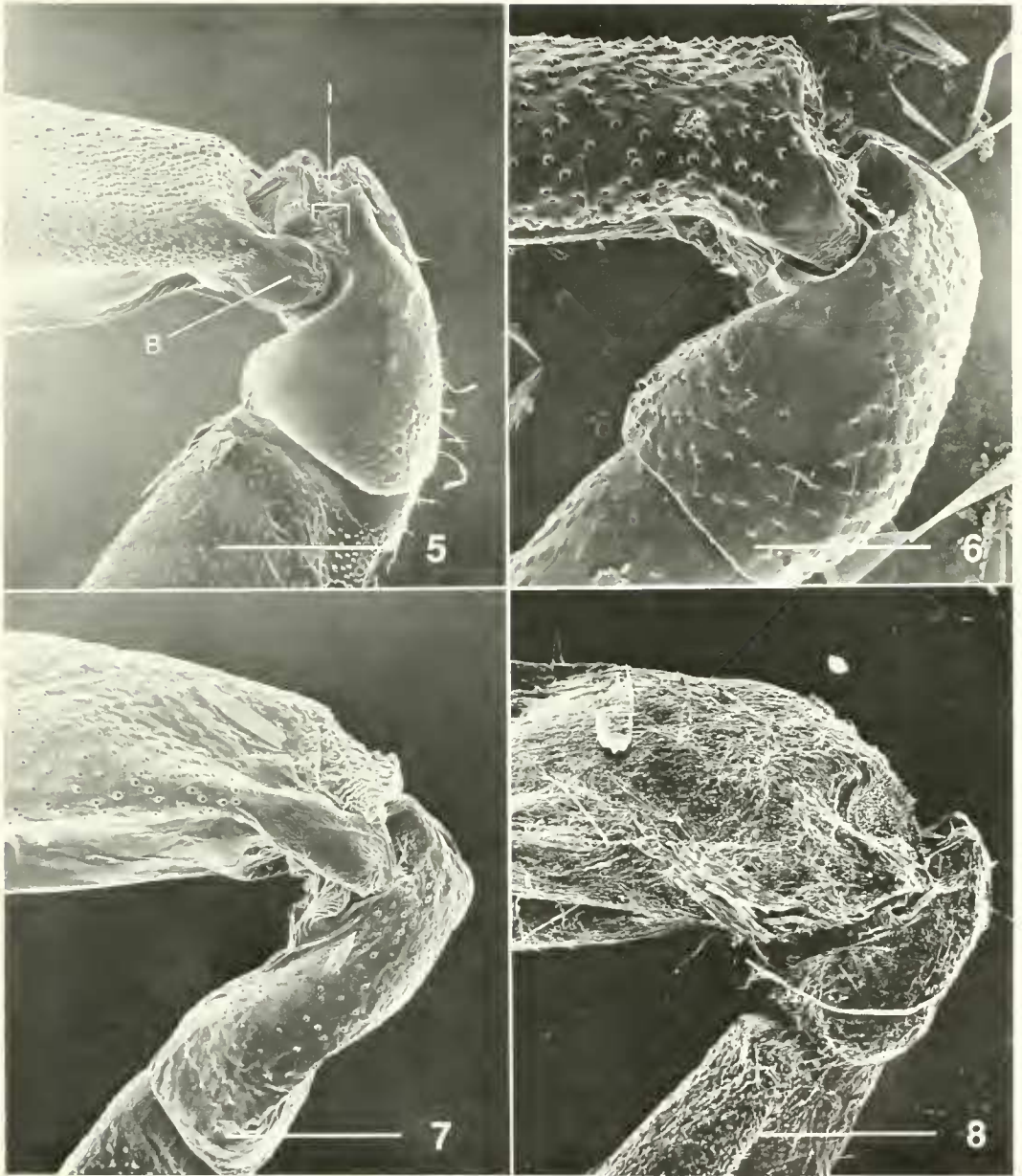
Lycaenidae (Theclinae, Polyommatainae, Lycaeninae): *Arawacus* Kaye, *Strymon* Hübner, *Calyeopsis* Scudder, *Evenus* Hübner, *Allosmaitia* Clench, *Hypaurotis* Scudder, *Axiocerses* Hübner, *Everes* Hübner, *Celastrina** Tutt, *Lycaena** Fabricius.

Female distribution.—*Hesperiidae:* *Hesperia* Fabricius, *Poanes*, *Thorybes* Scudder, *Erynnis* Schrank.

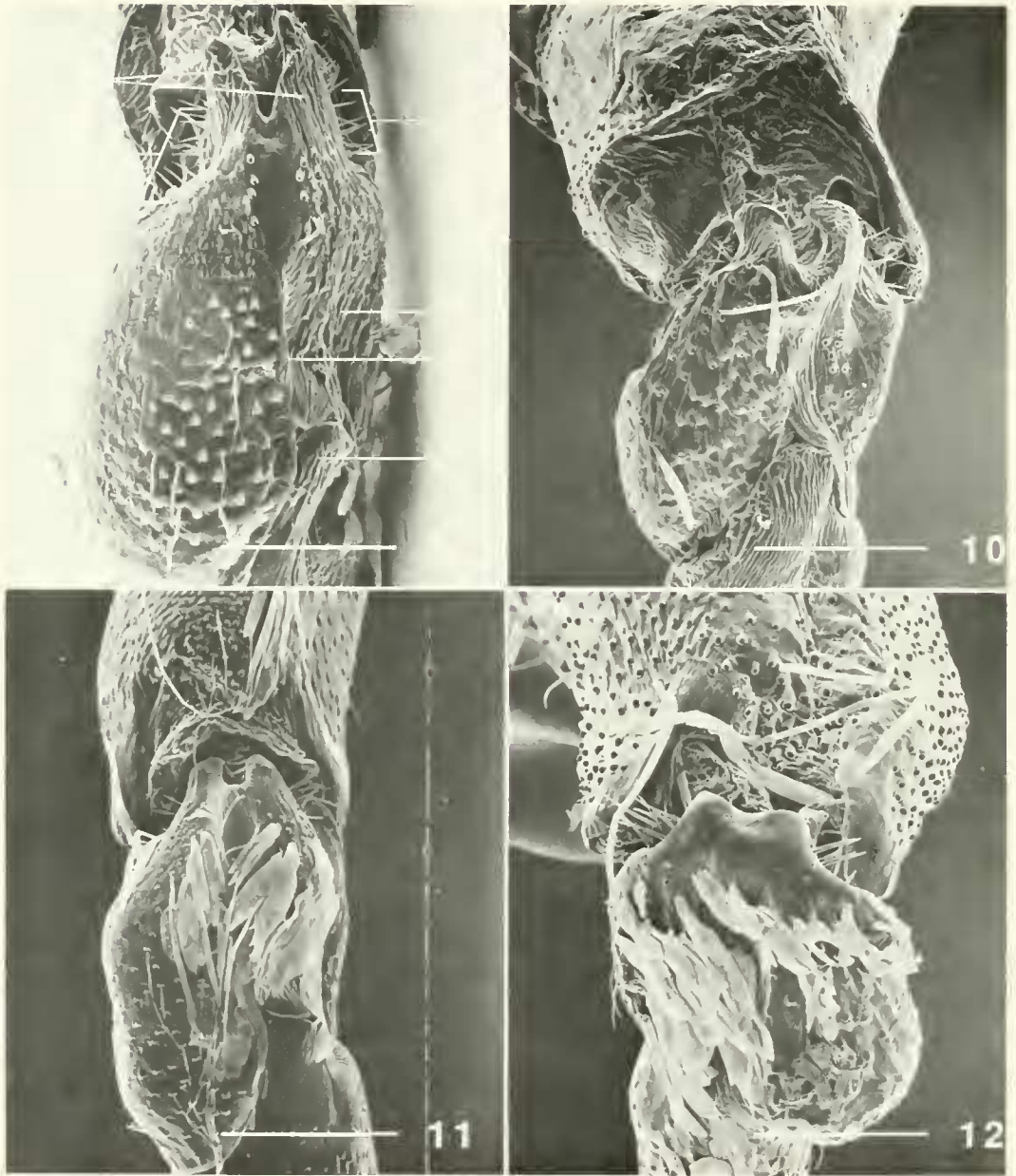
Papilionidae: *Papilio*, *Battus*, *Eurytides*, *Parnassius*.



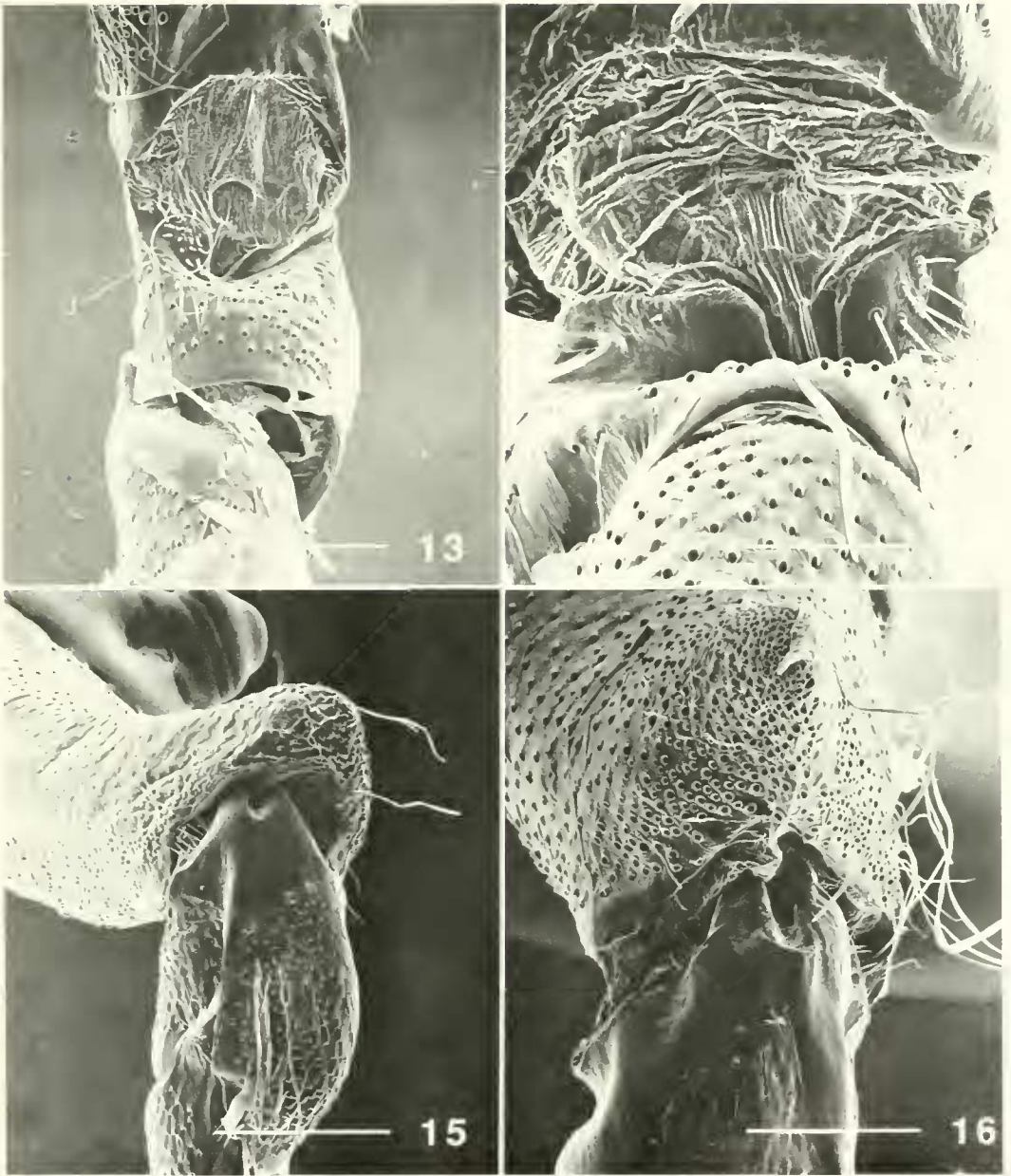
Figs. 1-4. Foreleg coxa, trochanter, and basal femur in lateral inside aspect. Coxa horizontal on top. Letters refer to structures in text. 1, *Eurema* male (Pieridae) (scale line 176 microns). 2, *Celastrina* female (Lycaenidae) (scale line 176 microns). 3, *Styx* female (Riodinidae) (scale line 176 microns). 4, *Libythea* female (Libytheidae) (scale line 150 microns).



Figs. 5-8. Foreleg coxa, trochanter, and basal femur in lateral outside aspect. Coxa horizontal on top. Letters refer to structures in text. 5, *Hesperia* female (Hesperiidae) (scale line 300 microns). 6, *Arawacus* male (Lycaenidae) (scale line 136 microns). 7, *Stalachtis* female (Riodinidae) (scale line 200 microns). 8, *Prepona* female (Nymphalidae) (scale line 380 microns).



Figs. 9–12. Foreleg trochanter in posterior aspect. Outside of leg to left except in *Danaus*. Letters refer to structures in text. 9, *Eurema* male (scale line 100 microns). 10, *Styx* female (scale line 150 microns). 11, *Libythea* female (scale line 150 microns). 12, *Danaus* female (Nymphalidae) (scale line 150 microns).



Figs. 13–16. Foreleg trochanter in anterior and posterior aspects. Letter refers to structure in text. 13, *Strymon* male (Lycaenidae) (scale line 136 microns), anterior aspect, outside of leg to right, coxa on top. 14, *Marpesia* female (Nymphalidae) (scale line 67 microns), anterior aspect, outside of leg to left, coxa on top. 15, *Pontia* male (Lycaenidae) (scale line 200 microns), posterior aspect, outside to right. 16, *Curetis* female (Lycaenidae) (scale line 150 microns), posterior aspect, outside to right.

Pieridae: *Eurema*, *Phoebis*, *Archonias* Hübner, *Pieris*.

Lycaenidae (*Theclinae*, *Polyommata*, *Lycaeninae*): *Eumaeus* Hübner, *Calycopis*, *Evenus*, *Axiocerses*, *Everes*, *Celastrina*,* *Lycaena*.*

Riodinidae (*Styginae*, *Hamearinae*, *Euselasiinae*, *Riodininae*): *Styx* Staudinger, *Laxita* Butler, *Hamearis* Hübner, *Hades* Westwood, *Stalachtis* Hübner, *Ancyluris* Hübner, *Mesosemia* Hübner, *Eurybia* Illiger.

Libytheidae: *Libythea** Fabricius.

Nymphalidae: *Dynamine** Hübner, *Prepona** Boisduval, *Doxocopa* Hübner, *Danaus* Kluk, *Marpesia** Hübner, *Chlosyne* Butler.

TYPE II

Morphology.—*Foreleg coxa*: This foreleg type retains structures A–K (Figs. 15–24), and its trochanter and femur do not differ from the Type I foreleg. It differs only in the shape of the coxa.

(L) The distal end of the coxa is arched dorsally, but there is a lot of quantitative variation within this character state. In some genera (*Allotinus* Felder & Felder, *Liphyra* Westwood, *Pentila* Westwood, *Ornipholidotos* Bethune-Baker, *Falcuna* Stempfffer & Bennett), the dorsal coxa forms a "hump" (Figs. 17, 21). In others (*Feniseca* Grote, *Poritia* Moore), the hump points dorso-posteriorly in a process that extends beyond (by approximately 0.1 mm) the articulation with the trochanter (Fig. 18). And in *Curetis*, the process extends well beyond (by approximately 0.3 mm) the trochanter (Figs. 19, 20, 22). It may be possible to code this variation in character states, but it would entail a more detailed study of the genera that have the Type II foreleg.

Male distribution.—*Lycaenidae* (*Lipteninae*, *Poritiinae*, *Liphyrinae*, *Miletinae*, *Curetinae*): *Pentila*, *Falcuna*, *Poritia*, *Allotinus*, *Feniseca*,* *Curetis*.*

Female distribution.—*Lycaenidae* (*Lip-*

teninae, *Poritiinae*, *Liphyrinae*, *Miletinae*, *Curetinae*): *Ornipholidotos*, *Falcuna*, *Poritia*, *Liphyra*, *Allotinus*, *Feniseca*,* *Curetis*.

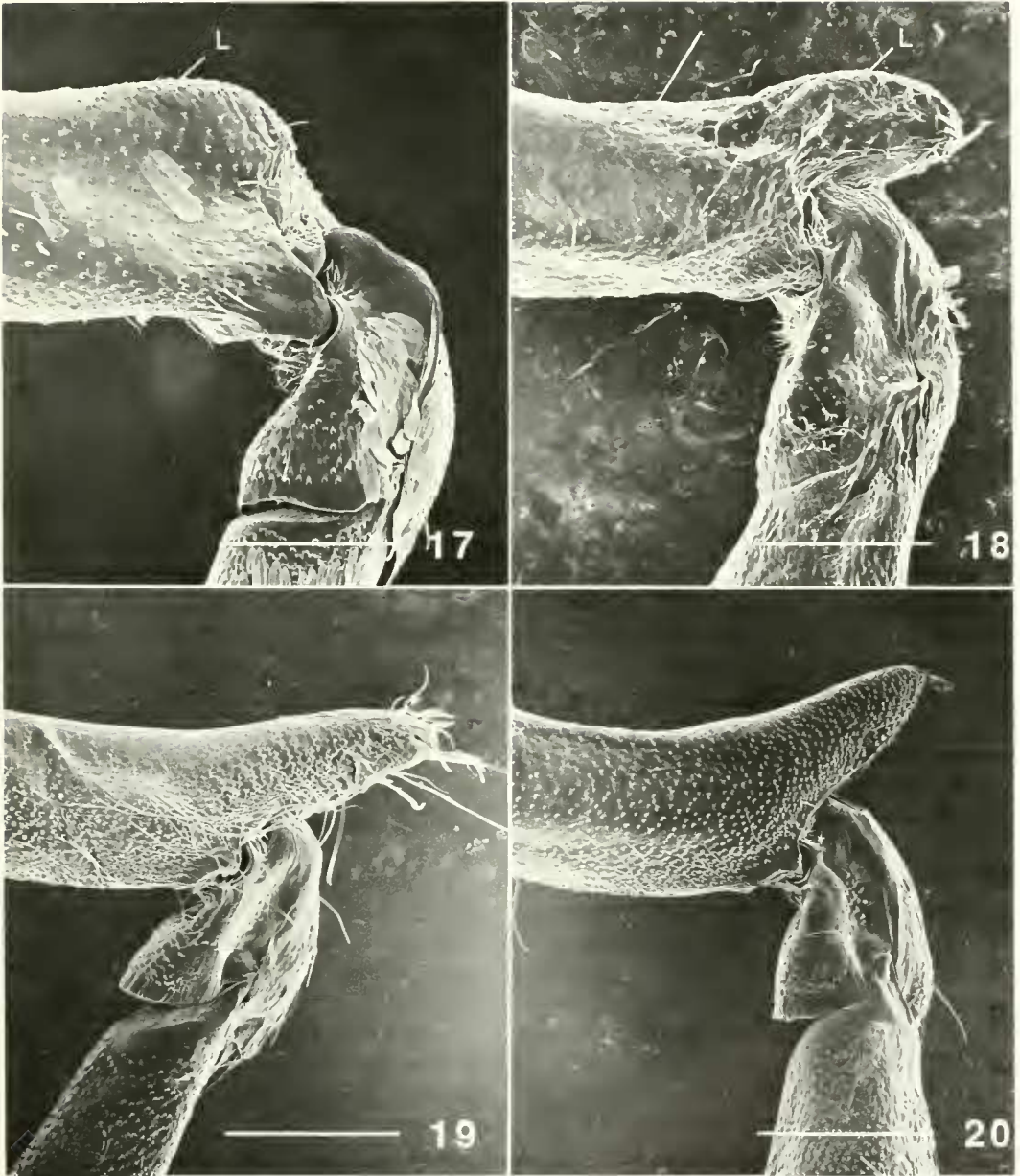
TYPE III

Morphology.—*Foreleg coxa and trochanter*: This foreleg type retains structures A–I and K (Figs. 25–39), and its femur does not differ from the Type II foreleg. It differs in the structure of the coxa and trochanter, and in that it is restricted to male forelegs.

(M) The dorsal, distal end of the foreleg coxa extends beyond the lateral processes of the coxa (structures A and B) and beyond the articulation of the trochanter in a process that is not arched dorsally (Figs. 25–26, 29–30, 33–34, 37–38).

(N) The cluster of trichoid sensilla on the inner anterior face of Type I and II foreleg trochanters (structure J) is lacking (Figs. 25, 28–29, 32–33, 36–37). This group of sensilla is lacking in all male butterflies that do not use their forelegs for walking, including the next two types. It is retained, however, in female nymphalids (Fig. 14), which do not use their forelegs for walking.

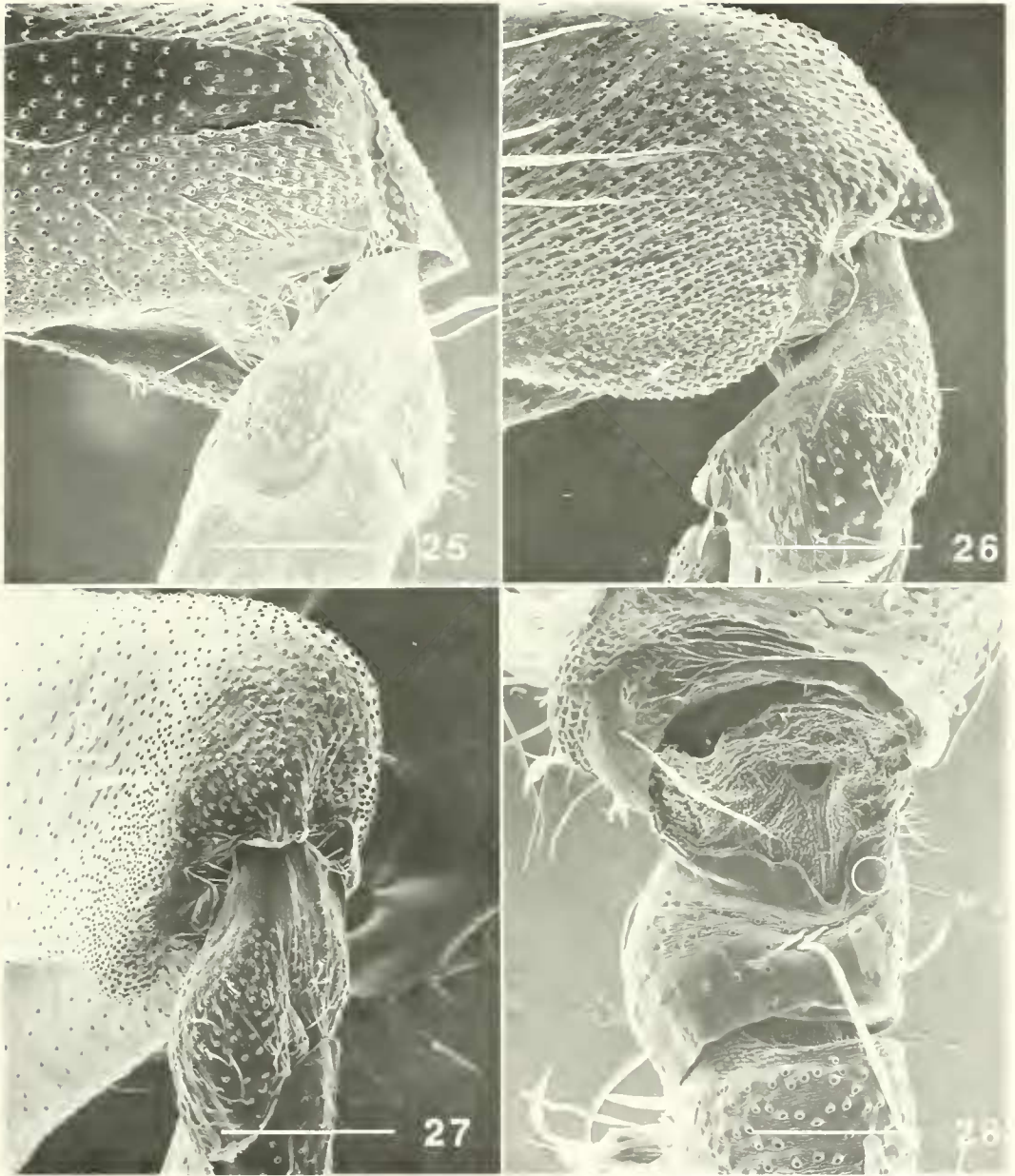
The Type III foreleg coxa shows two kinds of quantitative variation. First, the dorsal process of the coxa varies in length and shape. At one extreme, the dorsal process in *Laxita* and *Libythea* extends beyond the trochanter in a blunt process (approximately 0.10–0.15 mm) (Figs. 33–34, 37–38). At the other extreme in genera such as *Anartia* (Fig. 29), the dorsal process is rounded and barely extends beyond the trochanter (< 0.05 mm). Second, in some genera, such as *Doxocopa*, *Prepona*, and *Marpesia*, the coxa has a flap on the distal outside lateral side that "covers" the ventro-lateral process (Figs. 26–27). This flap is less well developed in *Dynamine* and *Memphis*, poorly developed in *Danaus*, and is apparently lacking in *Anartia*, *Libythea*, and *Laxita*. The trochanter is somewhat twisted in species with this flap so that the cluster of sensilla on the outside of the trochanter is more



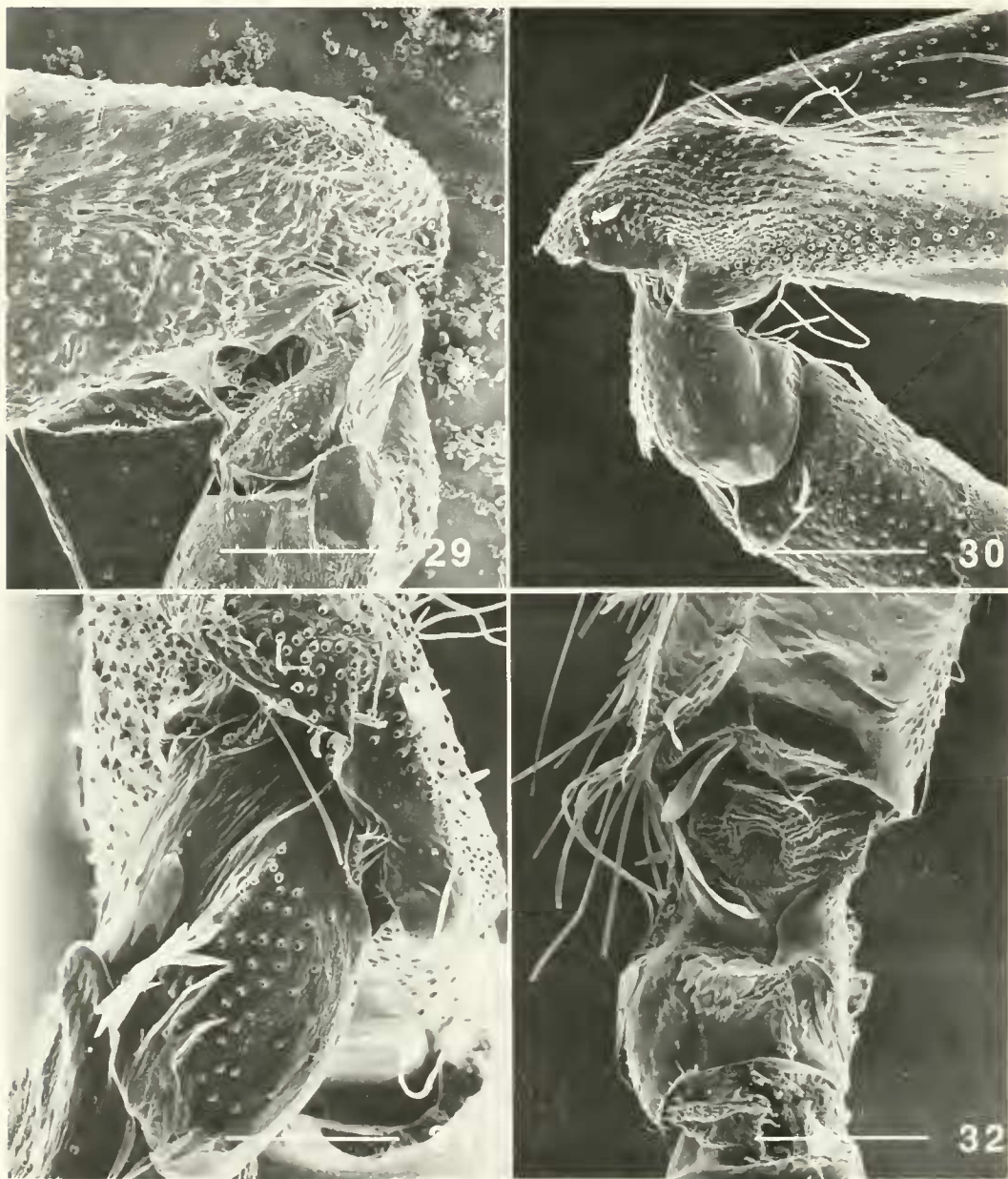
Figs. 17–20. Foreleg coxa and trochanter in inside lateral aspect. Coxa horizontal on top. Letter refers to structure in text. All Lycaenidae. 17, *Allotmus* male (scale line 200 microns). 18, *Femseca* female (scale line 176 microns). 19, *Curetis* male (scale line 380 microns). 20, *Curetis* female (scale line 380 microns).



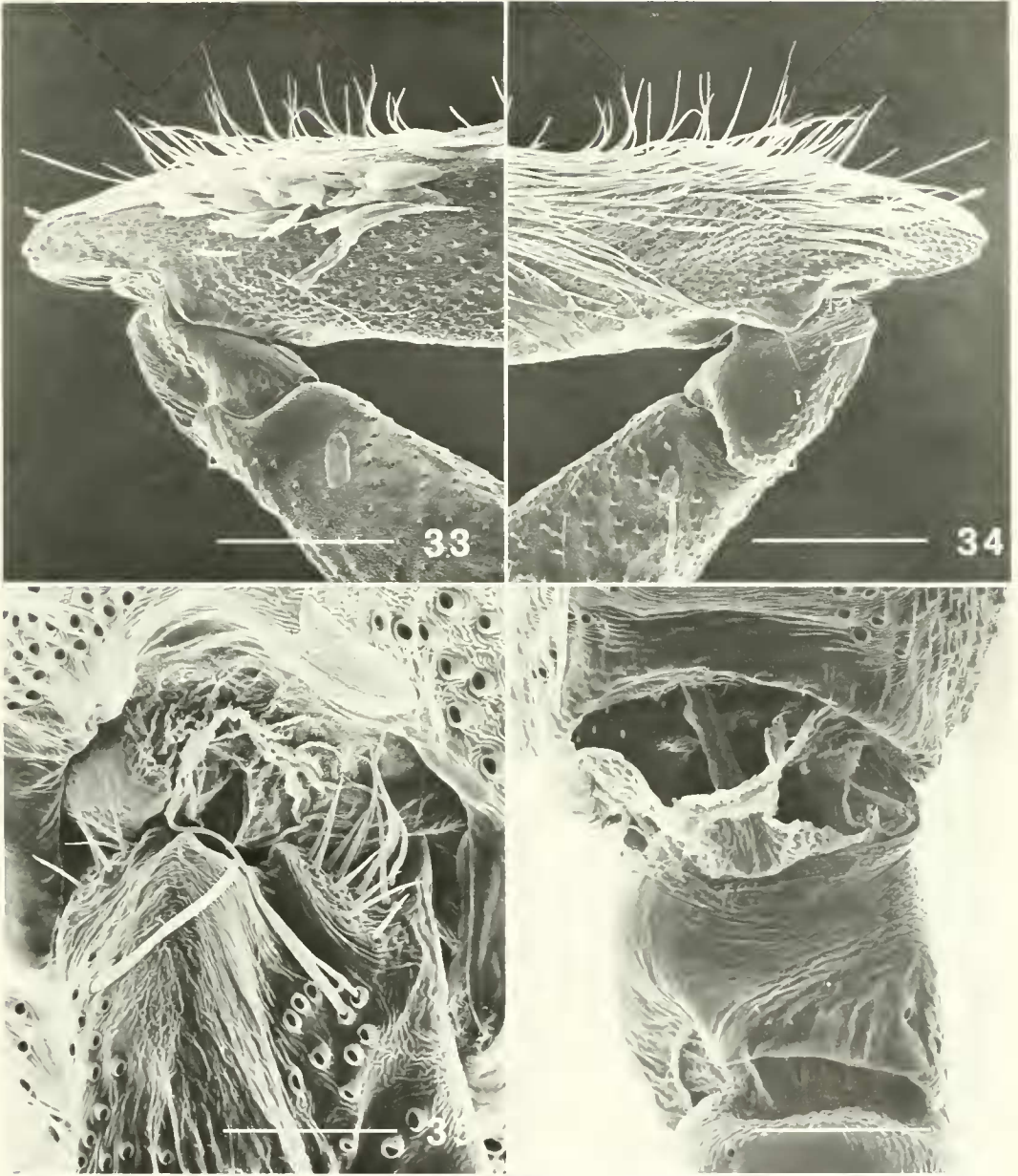
Figs. 21-24. Foreleg coxa and trochanter in outside lateral aspect and trochanter in anterior aspect. All Lycaenidae. 21, *Allotinus* male, coxa horizontal on top. (scale line 200 microns). 22, *Curetis* male, coxa horizontal on top, (scale line 380 microns). 23, *Feniseca* male, outside of leg to right (scale line 136 microns). 24, *Feniseca* female, outside of leg to left (scale line 136 microns).



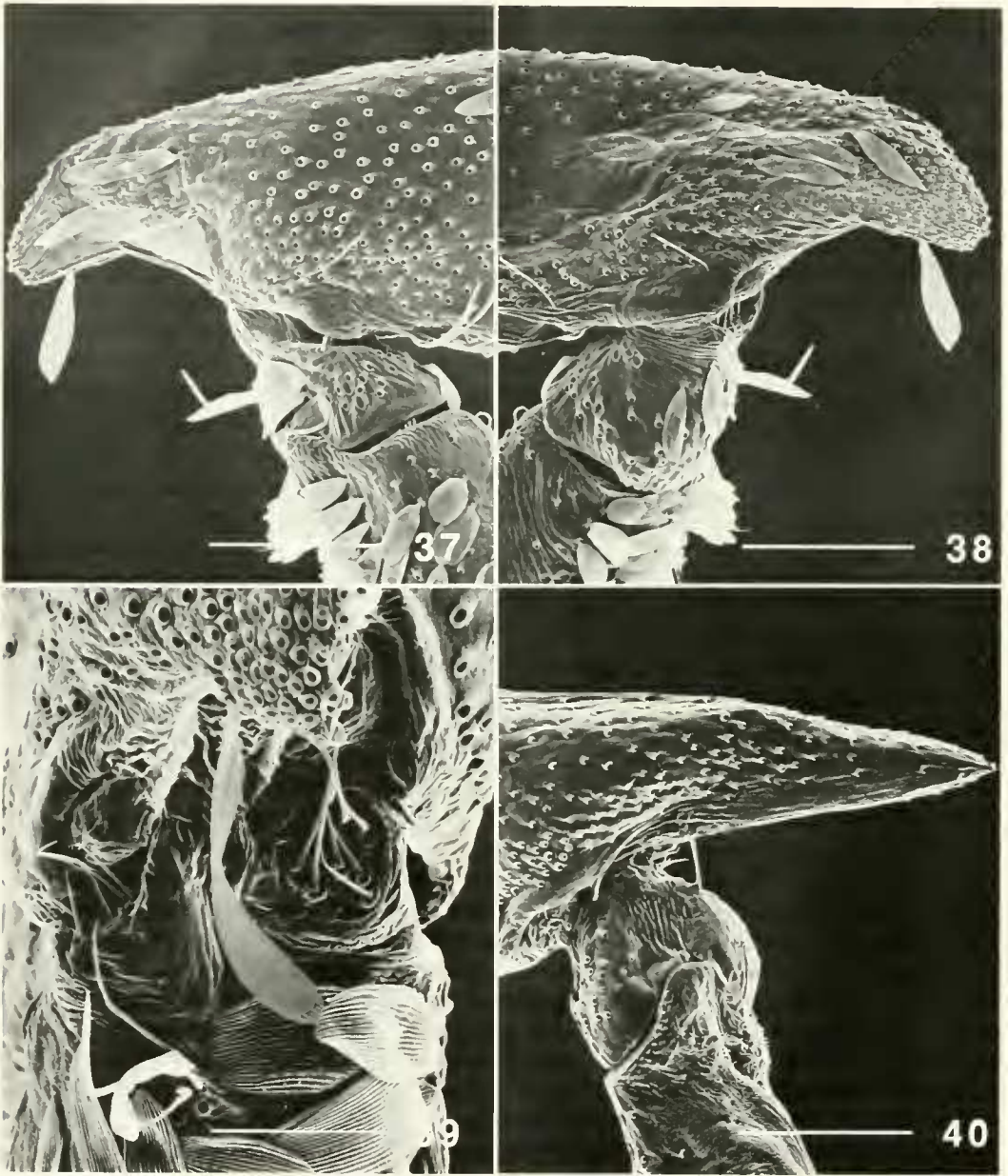
Figs. 25–28. Foreleg coxae and trochanters. Letter refers to structure in text. All Nymphalidae. 25, *Marpesia* male, inside lateral aspect with coxa horizontal on top (scale line 150 microns). 26, *Marpesia* male, outside lateral aspect with coxa horizontal on top (scale line 136 microns). 27, *Marpesia* male, posterior aspect with outside to left (scale line 150 microns). 28, *Memphis* male, anterior aspect with coxa on top and outside to left (scale line 136 microns).



Figs. 29–32. Nymphalid foreleg coxae and trochanters. 29, *Anartia* male, inside lateral aspect with coxa horizontal on top (scale line 150 microns). 30, *Dynamine* male, outside lateral aspect with coxa horizontal on top (scale line 150 microns). 31, *Dynamine* male, posterior aspect with outside to right (scale line 86 microns). 32, *Helicomius* male, anterior aspect with coxa on top and outside to right (scale line 136 microns).



Figs. 33–36. Foreleg coxa and trochanter of male *Libythea*. 33, Inside aspect of coxa and trochanter with coxa horizontal on top (scale line 176 microns). 34, Outside aspect of coxa and trochanter with coxa horizontal on top (scale line 176 microns). 35, Posterior aspect of trochanter (scale line 50 microns). 36, Anterior aspect of trochanter (scale line 60 microns).



Figs. 37–40. Foreleg coxa and trochanter and trochanter in posterior aspect (Riodinidae). 37, *Laxita* male, inside aspect with coxa horizontal on top (scale line 120 microns). 38, *Laxita* male, outside aspect with coxa horizontal on top (scale line 120 microns). 39, *Laxita* male, posterior aspect with outside to left (scale line 43 microns). 40, *Hamearis* male, inside lateral aspect (scale line 120 microns).

ventral than the cluster on the inside (Figs. 27, 31). A more extensive survey of Type III forecoxae might reveal phylogenetically useful qualitative variation within the Nymphalidae or between the Nymphalidae and Libytheidae + Riodinidae (*Hamearinae-Laxita*).

The second source of quantitative variation is the development of the dorsal prongs on the posterior trochanter (structure D). They are reduced to bumps in most genera, and in *Libythea* (Fig. 35), there is a third small bump between the two reduced prongs.

Male distribution.—*Riodinidae* (*Hamearinae* in part): *Laxita*.

Libytheidae: *Libythea*.*

Nymphalidae: *Hypanartia* Hübner, *Anartia* Hübner, *Heliconius** Kluk, *Pagyris** Boisduval, *Danaus*, *Marpesia*, *Dynamine**, *Callicore* Hübner, *Taygetis* Hübner, *Doxocopa*, *Prepona*, *Anaea* Hübner, *Memphis** Hübner.

TYPE IV

Morphology.—*Foreleg trochanter*: The coxa and femur do not differ qualitatively from the Type III foreleg (Figs. 40–48), but the trochanter does.

(O) The cluster of trichoid sensilla on the inside dorso-lateral posterior trochanter (structure H) is absent (Figs. 40–43, 47) while the Type III leg retains this cluster. Thus, the Type IV male foreleg trochanter is missing both clusters of trichoid sensilla on the inside, but retains the cluster on the outside (Figs. 40, 44, 46, 47).

All the Type IV forelegs that I examined under the SEM lacked the cluster of trichoid sensilla except for male *Ancyluris* and *Hamearis*, which had one sensillum (Figs. 40, 43). In the *Ancyluris* specimen, however, the other leg had no sensilla. I do not know if the presence of a single sensillum is a vestigial condition or if the sensillum is different from those in previous leg types clustered on that part of the trochanter. In either case, there is no cluster of trichoid sensilla.

The extension of the coxa beyond its articulation with the trochanter is highly variable in the Type IV foreleg. The amount that the coxa extends beyond the trochanter varies in the species that I examined from 0.23 mm in *Hamearis* and 0.28 mm in *Stalachtis* to about 0.80 mm in *Thisbe* Hübner. In *Thisbe*, the distal part of the coxa is longer than the basal part, but the opposite is true in *Stalachtis* and *Hamearis*. The male foreleg coxa of *Curetis* (Type II) extends beyond the trochanter more (approximately 0.30 mm) than in *Stalachtis* and *Hamearis*, but it is arched upwards whereas it is bluntly tapered in the riodinids.

The trochanter of the Type IV foreleg is sometimes shaped like a cylinder (Figs. 41–42), with the dorsal prongs completely reduced. In some genera, however, the trochanter is shaped much like that in Type III forelegs.

Male distribution.—*Riodinidae* (*Euselasiinae*, *Riodininae*, *Hamearinae* in part): *Hades*, *Emesis** Fabricius, *Thisbe*, *Stalachtis*, *Ancyluris*, *Mesosemia*, *Hamearis*.

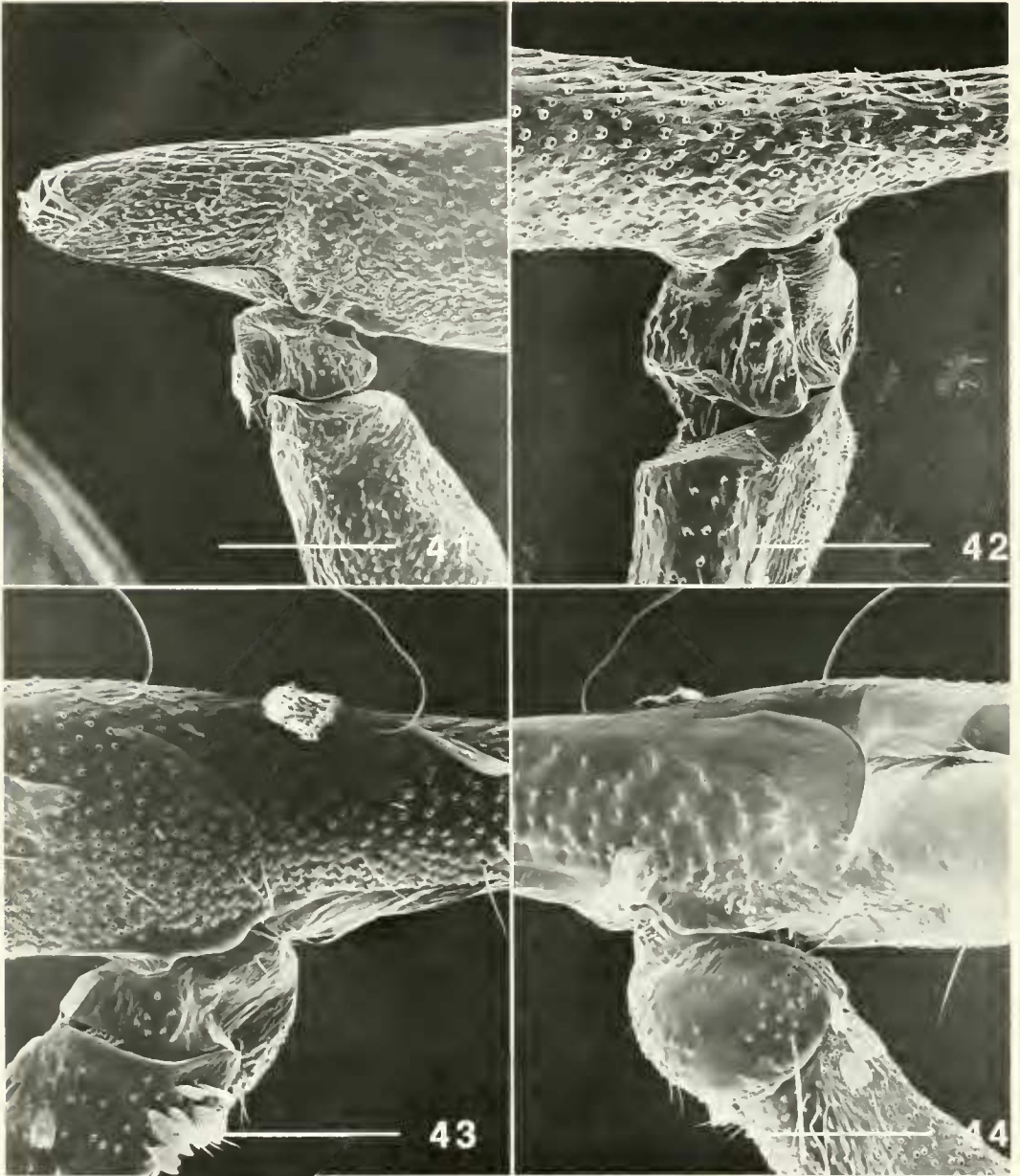
TYPE V

Morphology.—*Foreleg trochanter*: The foreleg trochanter again differs in the absence of a cluster of trichoid sensilla. Otherwise, the Type V foreleg retains the characters of the Type IV foreleg (Figs. 49–52).

(P) The trochanter lacks the cluster of trichoid sensilla on the outside dorso-lateral posterior surface (structure I) (Fig. 50).

I have examined with the SEM two male forelegs from one male specimen of *Styx*. Both forelegs have one trichoid sensillum on the trochanter in the general area where the outside posterior cluster of the trochanter occurs in other butterflies. It is unclear whether this single sensillum is a remnant of the cluster or a different kind of sensillum. In either case, the lack of a cluster is unique among the butterflies.

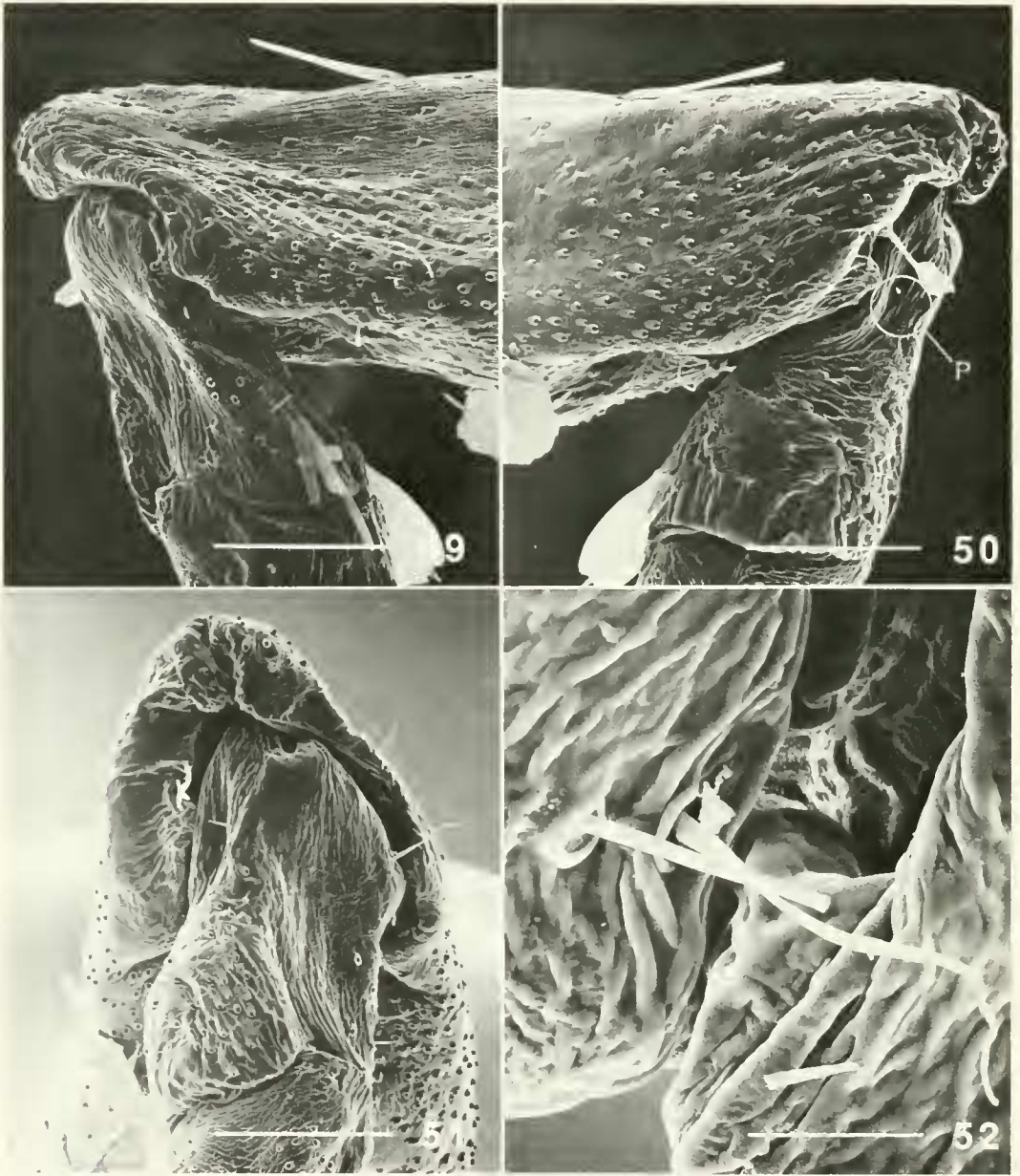
The inside dorsal cluster of the trochanter, which is absent or reduced to one sen-



Figs. 41–44. Lateral aspect of foreleg coxae and trochanters (Riodinidae). 41, *Stalactis* male, inside aspect with coxa horizontal on top (scale line 200 microns). 42, *Emesis* male, inside aspect with coxa horizontal on top (scale line 120 microns). 43, *Ancyluris* male, inside aspect with coxa on top (scale line 176 microns). 44, *Ancyluris* male, outside aspect with coxa on top (scale line 176 microns).



Figs. 45-48. Foreleg coxae and trochanters (Riodinidae). Letters refer to structures in text. 45, *Emesis* male, outside lateral aspect with coxa horizontal on top (scale line 300 microns). 46, *Stalactus* male, posterior aspect of dorsal trochanter showing cluster of trichoid sensilla on outside surface (scale line 30 microns). 47, *Hades* male, posterior aspect of trochanter, outside to left (scale line 100 microns). 48, *Ancylyuris* male, anterior aspect with coxa on top, outside to right (scale line 136 microns).



Figs. 49-52. Foreleg coxae and trochanters of *Styx* (Riodinidae). Letter refers to structure in text. 49, Inside lateral aspect with coxa horizontal on top (scale line 120 microns). 50, Outside lateral aspect with coxa horizontal on top (scale line 120 microns). 51, Posterior aspect of trochanter, outside to left (scale line 120 microns). 52, Enlargement of two setae on dorsal outside face of trochanter in Fig. 49 (scale line 15 microns).

sillum in the Type IV foreleg, is similarly reduced in *Styx*. One foreleg has a single trichoid sensillum while the other has two (Figs. 49, 52), but the sensilla are aberrant. On both legs, the sensillum socket is considerably larger than the "stalk" of the sensillum (Fig. 52). The space between the socket walls appears to be solid, and it is unclear whether the stalk goes through the integument. It appears to be a different kind of trichoid sensillum than those with foreleg Types I, II, and III, or it is possible that it is a vestigial structure.

The coxa has a dorsal posterior process that barely extends beyond the articulation of the trochanter (approximately 0.03 mm). In this regard, it is more similar to the Type III than the Type IV foreleg.

Male distribution.—*Riodinidae* (*Styginae*): *Styx*.*

CHARACTER MATRIX

I summarize the information above in a character matrix (Table 1), and derive a most parsimonious cladogram from it (Fig. 53). I use the Hesperidae as the outgroup for the Papilionoidea (Kristensen 1976, Scott 1985), and put an asterisk (*) next to the primitive character state for the papilionoids.

1. Foreleg coxa (A) in both sexes the dorsal surface is arched upwards at the distal end, may extend beyond the articulation with the trochanter, (B)* in both sexes the coxa tapers distally, but is not arched upwards nor does it extend beyond its articulation with the trochanter, (C) females as in the previous state, but in males the coxa tapers distally in a blunt process that is not arched upwards, but that extends beyond the articulation with the trochanter.

2. In males, the trochanter (A)* has a cluster (≥ 5) of trichoid sensilla on the anterior, inner lateral surface, (B) lacks this cluster of trichoid sensilla.

3. In males, the trochanter (A)* has a cluster of trichoid sensilla on the dorso-poste-

Table 1. Matrix of foreleg coxa and trochanter characters. Foreleg types and character states are given in the text. Lycaenidae #1: subfamilies Lycaeninae, Theclinae, and Polyommattinae, *sensu* Eliot (1973). Lycaenidae #2: Lipteninae, Poritinae, Liphyrinae, Miletinae, and Curetinae. Riodinidae #1: Hamearinae (*Laxita*), *sensu* Harvey (1987). Riodinidae #2: Hamearinae (*Hamearis*), Euselasiinae, and Riodininae. Riodinidae #3: Styginae.

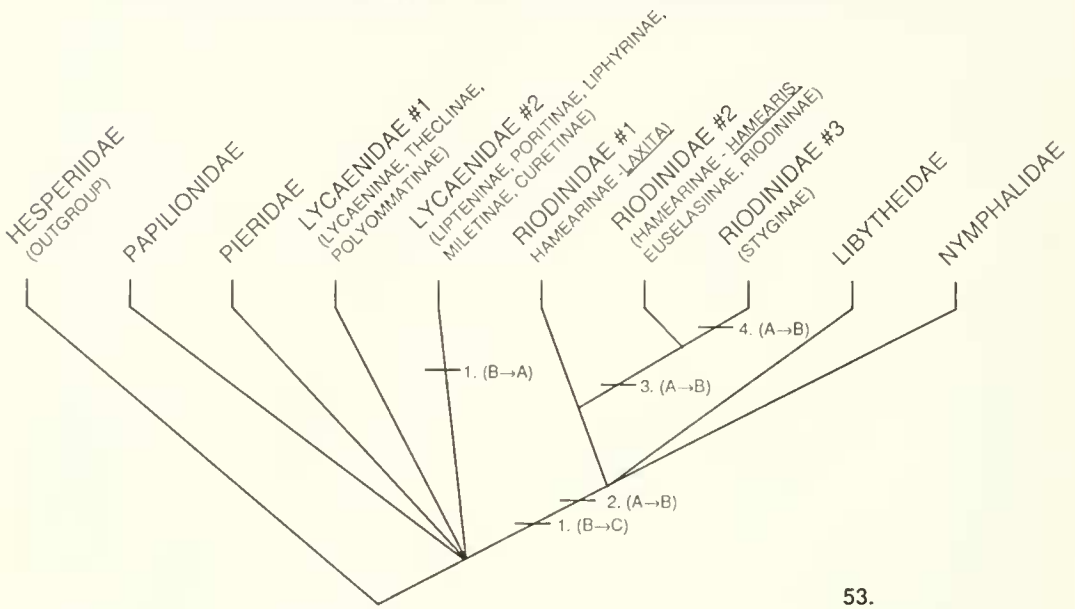
Taxon	Character			
	1	2	3	4
Type I male and female forelegs				
Hesperidae	B	A	A	A
Papilionidae	B	A	A	A
Pieridae	B	A	A	A
Lycaenidae #1	B	A	A	A
Type II male and female forelegs				
Lycaenidae #2	A	A	A	A
Type I female and type III male forelegs				
Libytheidae	C	B	A	A
Nymphalidae	C	B	A	A
Riodinidae #1	C	B	A	A
Type I female and type IV male forelegs				
Riodinidae #2	C	B	B	A
Type I female and type V male forelegs				
Riodinidae #3	C	B	B	B

rior inner lateral surface, (B) lacks this cluster of trichoid sensilla.

4. In males, the trochanter (A)* has a cluster of trichoid sensilla on the dorso-posterior outer lateral surface, (B) lacks this cluster of trichoid sensilla.

Of the three possible orders in which the three states of character 1 could have evolved, I chose transformation A-B-C. I provisionally rejected transformation B-A-C because it would require the female coxa to evolve a dorsal arch and then lose it. I provisionally rejected transformation B-C-A because it would require the evolution of sexual dimorphism in the coxa and then its loss. Other characters that provide evidence on the systematic placement of Lycaenidae #2 may also provide a test of my transformation hypothesis.

CLADOGRAM TO THE BUTTERFLIES



53.

Fig. 53. Cladogram to the butterfly families based on distribution of character states of the foreleg coxa and trochanter (Table 1). The numbers refer to characters and the letters to changes in character state.

DISCUSSION

Foreleg coxa and trochanter character states are qualitatively invariant within previously recognized butterfly families except for the Lycaenidae and Riodinidae, which is significant in two respects. First, the Lycaenidae + Riodinidae are sometimes lumped in a presumably homogeneous and monophyletic taxon (e.g. Kristensen 1976), perhaps because they are rich in species whose morphology is poorly known. The results in this paper and others (Robbins 1987, 1988) indicate that for leg characters, at least, there is a great deal of morphological variation among the Lycaenidae and Riodinidae. Second, the lack of variation within the HesperIIDae, Papilionidae, Pieridae, Libytheidae, and Nymphalidae in the structure of foreleg coxae and trochanters lends credence to their stability as evolutionary characters (Kluge and Farris 1969).

The distribution of foreleg coxae and tro-

chanters—summarized in the character matrix (Table 1)—provides evidence for four presumably monophyletic taxa among the butterflies (Fig. 53). The first taxon is the riodinid subfamily Styginae, which has uniquely evolved state B of character 4 (Fig. 53). I have not yet had the opportunity to examine the legs of the monotypic riodinid genera *Petrocerus* Callaghan and *Corrachia*, but their forecoxae are apparently similar to that of *Styx* (Callaghan 1979, Harvey 1987) in that they do not extend well beyond the articulation with the trochanter.

The second monophyletic taxon is a combination of the riodinid subfamilies Euselasiinae, Riodininae, Styginae, and the genus *Hamearis* of the Hamearinae (Fig. 53). It is characterized by the evolution of state B of character 3. This result has not been proposed previously, and suggests that the New World Riodinidae plus *Hamearis* may be a monophyletic group. The male foreleg

coxa and trochanter of the Old World riodinid *Laxita* (Hamearinae) does not differ qualitatively from those of Libytheidae or Nymphalidae. Harvey (1987) considered the Hamearinae to be monophyletic because they share a posterior pointing beaked uncus in the male genitalia. My results conflict with this classification, but clearly they are preliminary since I have examined only two genera in the Hamearinae.

The third monophyletic taxon is a combination of the lycaenid subfamilies Lipteninae, Poritinae, Liphyrinae, Miletinae, and Curetinae (Fig. 53). It is characterized by the evolution of state A in males and females (character 1). Again, this combination of subfamilies has not been previously recognized as monophyletic, and is inconsistent with Scott's (1985) phylogeny of the lycaenid subfamilies. If the transformation of character 1 is B-A-C, however, then this group could be paraphyletic. It consists of hundreds of species restricted to the Old World except for a single Nearctic species, *Feniseeca tarquinus* Fabricius.

The last monophyletic group is Riodinidae + Libytheidae + Nymphalidae, characterized by the evolution of state C of character 1 and state B of character 2 (Fig. 53). I have gotten the same phylogenetic result using other leg characters (Robbins 1987). Since all other published phylogenies (Ehrlich 1958, Kristensen 1976, Scott 1985) consider the Lycaenidae + Riodinidae to be a monophyletic group—in contradiction to my results—either there has been a great deal of convergence among leg characters or the previous phylogenies have been based on poorly analyzed characters whose distributions are also poorly known.

The results in this paper partly confirm and partly contradict the morphological results of Ehrlich (1958b). They contradict Ehrlich's report that the male foreleg coxa of *Styx* does not extend beyond the trochanter, but its extension is smaller than in most other riodinids, which is probably what

Ehrlich observed. Further, similar short extensions apparently occur in some other riodinids, specifically *Corrachia* (Harvey 1987) and *Petrocerus* (Callaghan 1979). Ehrlich's finding that the foreleg coxa extends slightly below the articulation with the trochanter in male *Curetis* (Lycaenidae) is correct, but incomplete. He did not note that the forecoxa also extends beyond the articulation with the trochanter in male Nymphalidae, Libytheidae, and *Styx* as well as both sexes in some lycaenids with a Type II forecoxa (*Curetis*, *Feniseeca*, *Poritia*).

My results are inconsistent with Scott's (1985) phylogenetic hypothesis that *Curetis* and Riodinidae (his Riodininae) form a monophyletic group. He supported this hypothesis in part by noting that the male forecoxa of these two groups extends beyond the articulation with the trochanter. However, this "character state" occurs in many other butterflies, as I have noted. Further, the forecoxa of *Curetis* is qualitatively distinct from that in riodinids. It is arched dorsally, extends beyond the articulation with the trochanter in both sexes, and its trochanter retains a cluster of sensilla on its inside anterior face. The forecoxa of riodinids is not arched dorsally, extends beyond the trochanter only in males, and its trochanter does not retain the cluster of sensilla on its inside anterior face. Thus, the similarity in shape of the forecoxae of riodinids and *Curetis* is superficial, and Scott's hypothesis would appear to be incorrect.

ACKNOWLEDGMENTS

I thank Don Harvey for numerous discussions and exchange of pertinent information. I thank John Eliot, Don Harvey, Gerardo Lamas, James Scott, and an anonymous reviewer for critically reading and commenting on the paper. I thank Brian Kahn and Susann Braden for working with me on the SEM. I thank Gerardo Lamas for loaning me a male specimen of *Styx infernalis*. I thank Phil Ackery and Dick Vane-

Wright for loaning me Ehrlich's dissection of a male *S. infernalis*.

LITERATURE CITED

- Bates, H. W. 1861. Contributions to an insect fauna of the Amazon Valley.—Lepidoptera—Papilionidae. *J. Entomol.* 1: 218–245.
- Borror, D. J., D. M. De Long, and C. A. Triplehorn. 1981. An introduction to the study of insects. Fifth ed. Saunders College, Philadelphia. 827 pp.
- Callaghan, C. J. 1979. A new genus and a new subspecies of Riodinidae from southern Brasil. *Bull. Allyn Mus.* #53: 7.
- Ehrlich, P. R. 1958a. The integumental anatomy of the monarch butterfly *Danaus plexippus* L. (Lepidoptera: Danaidae). *Univ. Kan. Sci. Bull.* 38: 1315–1349.
- . 1958b. The comparative morphology, phylogeny and higher classification of the butterflies (Lepidoptera: Papilionoidea). *Univ. Kan. Sci. Bull.* 39: 305–370.
- Eliot, J. N. 1973. The higher classification of the Lycaenidae (Lepidoptera): A tentative arrangement. *Bull. Brit. Mus. (Nat. Hist.) Entomol.* 28: 371–505.
- Ford, E. B. 1945. Butterflies. *The New Naturalist*, Collins, London. 368 pp.
- Godman, F. D. and O. Salvin. 1879–1901. *Biologia Centrali-Americana*. Insecta. Lepidoptera-Rhopalocera. Published by the authors, Vol. 1. 487 pp.
- Harvey, D. J. 1987. The higher classification of the Riodinidae (Lepidoptera). Ph.D. Dissertation, Univ. Texas, Austin, Texas. 216 pp.
- Kluge, A. G. and J. S. Farris. 1969. Quantitative phyletics and the evolution of Anurans. *Syst. Zool.* 18: 1–32.
- Kristensen, N. P. 1976. Remarks on the family-level phylogeny of butterflies (Insecta, Lepidoptera, Rhopalocera). *Z. Zool. Syst. Evolut.-forsch.* 14: 25–33.
- Robbins, R. K. 1987. Logic and phylogeny: A critique of Scott's phylogenies to the butterflies and macrolepidoptera. *J. Lepid. Soc.* 41: 214–216.
- . 1988. Male foretarsal variation in Lycaenidae and Riodinidae (Lepidoptera), and the systematic placement of *Styx infernalis*. *Proc. Entomol. Soc. Wash.* (Submitted).
- Scott, J. A. 1985. The phylogeny of butterflies (Papilionoidea and Hesperioidea). *J. Res. Lepid.* 23: 241–281.
- . 1986. *The butterflies of North America*. Stanford University Press, Stanford, 583 pp.
- Stichel, H. 1910–1911. Lepidoptera Rhopalocera, Fam. Riodinidae, Allgemeines—Subfam. Riodininae. Fascicule 112. In P. Wylsman, ed., *Genera Insectorum*, V. Vertheuil & L. Desmet, Bruxelles. 452 pp.